Anatomy and Physiology of Odontocete Echolocation

Ted W. Cranford, Ph.D.
Quantitative Morphology Consulting
2674 Russmar Drive, San Diego, CA 92123-3422
phone: (619) 226-7944 fax: (619) 226-7944 email: tcranfor@mail.sdsu.edu

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LONG-TERM GOALS

The primary goal for this effort is to distill the results of several years of research into media that can be digested by the scientific community and the public.

OBJECTIVES

Two major objectives were to: (1) prepare at least three peer-reviewed professional publications (PPPs), and (2) transform key results from the PPPs into graphical displays for the World Wide Web.

APPROACH

All PPPs have been written by Dr. Ted W. Cranford and his coauthors. The PPPs prepared in this effort will be reviewed by collaborators and revisions completed by Dr. Cranford. The development of web pages will be contracted out.

WORK COMPLETED

The accomplishments have far exceeded the goals and objectives. Eight papers were produced for publication, surpassing the original goal of three peer reviewed papers submitted to scientific journals. A ninth manuscript has been generated and will soon be submitted. All others are in various stages of review, revision, acceptance, or publication. The design and construction of the parallel website has suffered a few setbacks but the process is now moving forward.

The peer-reviewed papers generated from this grant are as follows:

1. Anatomic Geometry of Sound Transmission and Reception in Cuvier's Beaked Whale (*Ziphius cavirostris*); The Anatomical Record. [In press, refereed].
Cranford, Ted W., M. McKenna, M. Soldevilla, S.M. Wiggins, J. Goldbogen, R. Shadwick, P. Krysl, J. St. Leger, and J.A. Hildebrand

Abstract: This study uses remote imaging technology to quantify, compare, and contrast the cephalic anatomy between a neonate female and a young adult male Cuvier's beaked whale. Primary results reveal details of anatomic geometry with implications for acoustic function and diving. Specifically, we describe the juxtaposition of the large pterygoid sinuses, a fibrous venous plexus, and a lipid-rich pathway that connects the acoustic environment to the bony ear complex. We surmise that the large pterygoid air sinuses are essential adaptations for maintaining acoustic isolation and auditory acuity of the ears at depth. In the adult male, an acoustic waveguide lined with pachyosteosclerotic bones is apparently part of a novel transmission pathway for outgoing biosonar signals. The anatomy of this transmission path resembles an upside-down sperm whale nose and may be its functional equivalent but the homologous relationships between forehead structures are equivocal.

2. Evaluation of Postmortem Changes in Tissue Structure in the Bottlenose Dolphin (*Tursiops truncatus*); The Anatomical Record, 290:1023–1032 (2007). [Published, refereed].
Mckenna, M.F., J.A. Goldbogen, J. St. Leger, J.A. Hildebrand, and **Ted W. Cranford**

Abstract: Postmortem changes in geometry, density, and sound speed within organs and tissues (melon, bone, blubber, and mandibular fat) of the dolphin head were evaluated using CT scans of live and postmortem bottlenose dolphins (Tursiops truncatus). Specimens were classified into three different treatment groups: live, recently dead, and frozen followed by thawing. Organs and tissues in similar anatomical regions of the head were compared in CT scans of the specimens to identify postmortem changes in morphology. In addition, comparisons of Hounsfield units in the CT scans were used to evaluate postmortem changes in the density of melon, bone, blubber, and mandibular fat. Sound speed measurements from melon, blubber, connective tissue, and muscle were collected from fresh and frozen samples in the same specimen to evaluate effects due to freezing and thawing process on sound speed measurements. Similar results in tissue and organ geometry, density, and sound speed measurements suggested that postmortem material is a reliable approximation for live melon, bone, blubber, muscle, connective tissue, and mandibular fat. These results have implications for examining viscoelastic properties and the accuracy of simulating sound transmission in postmortem material.

3. Acoustic Radiation from the Head of Echolocating Harbor Porpoises (*Phocoena phocoena*); The Journal of Experimental Biology, 209: 2726-2733 (2006). [Published, refereed].
Au, W.W.L., R.A. Kastelein, K.J. Benoit-Bird, **Ted W. Cranford**, and M.F. McKenna

Abstract: An experiment was conducted to investigate the sound pressure patterns on the melon of odontocetes by using four broadband hydrophones embedded in suction cups to measure echolocation signals on the surface of the forehead of two harbor porpoises (*Phocoena phocoena*). It has long been hypothesized that the special lipids found in the melon of odontocetes, and not in any other mammals, focus sounds produced in the nasal region that then propagate through the melon, producing a beam that is directional in both the horizontal and vertical planes. The results of our measurements supported the melon-focusing hypothesis, with the maximum click amplitude, representing the axis of the echolocation beam, located approximately 5.6–6.1·cm from the edge of the animal's upper lip along the midline of the melon. The focusing is not sharp but is sufficient to produce a transmission beam of about 16°. Click amplitude dropped off rapidly at locations away from the location of site of maximum amplitude. Based on comparisons of forehead anatomy from similar sized porpoises, the beam axis coincided with a pathway extending from the phonic lips through the axis of the low-density/low sound velocity lipid core of the melon. The significant interaction between click number and hydrophone position suggests that the echolocation signals can take slightly different pathways through the melon, probably as a result of how the signals are launched by the production mechanism and the position of the acoustically reflective air sacs.

4. Lagrangian Finite Element Treatment of Transient Vibration/Acoustics of Biosolids Immersed in Fluids; International Journal for Numerical Methods in Engineering [In press, refereed].
Krysl, P., **Ted W. Cranford**, and J.A. Hildebrand

Abstract: Superposition principle is used to separate the incident acoustic wave from the scattered and radiated waves in a displacement-based finite element model. An absorbing boundary condition is applied to the perturbation part of the displacement. Linear constitutive equation allows for inhomogeneous, anisotropic materials, both fluids and solids. Displacement-based finite elements are used for all materials in the computational volume. Robust performance for materials with limited compressibility is achieved using assumed-strain nodally-integrated simplex elements, or incompatible-mode brick elements. A centered-difference time-stepping algorithm is formulated to handle general damping accurately and effciently. Verification problems (response of empty steel cylinder immersed in water to a step plane wave, and scattering of harmonic plane waves from an elastic sphere) are discussed for assumed-strain simplex and for voxel-based brick finite element models. A voxel-based modeling scheme for complex biological geometries is described, and two illustrative results are presented from the bioacoustics application domain: reception of sound by the human ear, and simulation of biosonar in beaked whales.

5. Observation and Analysis of Dolphin Sonar Signal Generation; Journal of Experimental Biology. [submitted].
Cranford, Ted W., W.R. Elsberry, W.G. Van Bonn, J.A. Carr, M.S. Chaplin, D.J. Blackwood, D.A. Carder, T. Kamolnick, M. Todd, S.H. Ridgway

Abstract: Indirect evidence exists for multiple sonar signal generators in odontocetes. Direct evidence was collected from three bottlenose dolphins by simultaneously observing nasal tissue motion, internal nasal cavity pressure, and external acoustic pressure. A methodological system based on high-speed video endoscopy revealed tissue motion at both pairs of phonic lips, while two hydrophones measured acoustic pressure during biosonar target discrimination. Small catheters measured pneumatic pressure changes at various locations within the complex array of nasal air passages and in the basicranial air spaces. Records clearly demonstrate that acoustic pulses can be generated at the phonic lips on the left and right sides, independently or simultaneously. We have only seen whistles generated at the phonic lips on the left side. Air pressure in both bony nasal passages rises and falls together, even if the activity patterns at the two pairs of phonic lips are different. Increasing pulse repetition rate or sound pressure level, and whistle production are all normally accompanied by increasing nasal air pressure. Clicks occur coincident with one oscillatory cycle of the phonic lips. Changes in the click repetition rate and cycles of the phonic lips are simultaneous, indicating these events are unequivocally coupled. These observations settle a long-standing controversy over the site of biosonar signal generation in odontocetes.

6. Measuring Intranarial Pressure during Biosonar; Journal of the Acoustical Society of America. [submitted].
W.R. Elsberry, **Ted W. Cranford**, D.J. Blackwood, D.A. Carder, W.G. Van Bonn, J.A. Jeffress, and S.H. Ridgway

Abstract: Physiological measurements of sound production in odontocetes during biosonar tasks have implications for bioenergetics, communication, and evolution. Intranarial pressure was measured in bottlenose dolphins during a biosonar target recognition task. A whistle response was paired with a stainless steel water-filled sphere target. Acoustic and physiologic data were simultaneously recorded via analog to digital computer-based instrumentation. Two out of three subjects performed significantly above chance on the biosonar task. Subjects increased intranarial pressure to emit biosonar clicks and whistles. Such pressurization events had significantly different average intranarial pressure, such that those events which were associated only with biosonar clicks were lower than those

which were associated with both biosonar clicks and whistle responses. Average intranarial pressure was highest for pressurization event that only included whistle responses.

7. Acoustic pathways revealed: simulated sound transmission and reception in Cuvier's beaked whale (*Ziphius cavirostris*) using the vibro-acoustic toolkit; Bioinspiration & Biomimetics [submitted].
Ted W. Cranford, Petr Krysl, and John A. Hildebrand

Abstract: Simulated sound sources placed inside and outside of an adult male Cuvier's beaked whale (*Ziphius cavirostris*) have revealed pathways for acoustic propagation into and out of the head. Sound sources located at the left and right phonic lips produce beams that converge just outside the head and slightly right of the midline. This result supports the notion that dual sonar sources interfere constructively to form a sonar beam in front of the animal. The most important questions regarding sound exposure concern the pathways by which sounds reach the hearing apparatus. A 40 kHz planar wave that approaches from in front of the animal may be transmitted through the lower jaw by flexural wave coupling. The simulations also indicate a new "gular pathway" for sound reception. Propagated sound pressure waves enter the head from below and between the lower jaws, continuing toward the bony ear complexes through the internal mandibular fat bodies.

8. Dolphin Ear Trumpet Discovered: A New Acoustic Window into the Odontocete Ear; Nature. [submitted].
Ted W. Cranford and M. Amundin

Abstract: The auditory pathway for high-frequency biosonar signals in toothed whales passes from the aquatic environment into fatty channels within the hollow mandibles to the bony hearing complex (Norris 68). This pathway is an evolutionary novelty (Oelschlager 1986, Fleischer 1980). It partially compensates for the impedance mismatch experienced by whale ancestors as they moved from hearing in air to water, creating a diminished capacity for amplitude sensitivity and directional hearing. Unique lipid channels define the sound propagation pathways into and out of the odontocete head (Norris 68, Ketten 1992, 2000) but there has never been an explanation for how high frequency vibrations pass from the low density fatty tissue into the high density bones comprising parts of the auditory apparatus. Here we identify an acoustic portal and a plausible mechanism by which ultrasound passes into the transduction apparatus of hearing. The discovery of this new acoustic window in the odontocete auditory apparatus offers a vantage point from which to decipher the mechanisms of auditory filtering, beam forming, and transduction. It also provides a unique perspective on the evolution of the acoustico-mechanical functions of hearing in odontocetes.

9. Using Industrial CT Scanners to Study the Anatomic Geometry of Large Whales; This manuscript is in the final stages of preparation.
Cranford, Ted W.

Abstract: The anatomic geometry of large cetaceans is poorly understood and little additional knowledge has accumulated since the heydays of the whaling industry. The recent spate of beaked whale deaths associated with exposure to high-intensity sound has produced a need to understand the interaction between whales and the acoustic environment. Technological advances combined with a newly developed means of stabilizing large specimens produce an innovative methodology for capturing *in situ* anatomy of large whales. The techniques maintain specimens in a frozen state during a lengthy X-ray scanning process. Advancements in the size, capacity, and computational power of

industrial X-ray CT scanners have produced high-resolution scans from the heads of four large specimens: A neonate fin whale (*Balaenoptera physalus*); an adult Cuvier's beaked whale (*Ziphius cavirostris*), an adult Baird's beaked whale (*Berardius bairdii*), and an adult killer whale (*Orcinus orca*).

RESULTS

There are several meaningful results contained in the papers prepared for this report. One paper contains the first description of anatomic geometry in a beaked whale (#1), providing a foundation for understanding and modeling sound propagation in the head. Two other papers (#4 & #7) report on the development of acoustic modeling techniques and the results of the first simulations that show the probable pathways for sound entering and exiting the ziphiid head. Three more contributions (#2, #8, & #9) validate our techniques of using postmortem specimens to study acoustic function in odontocetes. The remaining three papers (#3, #5, & #6) are all based on measurements and observations from live animals that expand the breadth of our understanding of biosonar in odontocetes and serve as a check on our models, simulations, and extrapolations of function from structure. Clearly, the most significant results concern the recent development of FEA acoustic simulation tools.

IMPACT/APPLICATIONS

These FEA (finite element analysis) techniques appear to be returning expected and unanticipated results that are apparently robust. These tools will allow us to probe new and previously unanswerable or unapproachable questions. Perhaps the most significant impact will follow from the potential widespread taxonomic applicability. Beyond cetaceans, these tools could be used to simulate sound propagation in virtually any aquatic vertebrate. In addition, our studies of odontocete acoustic anatomy and its physiologic function will undoubtedly lead us to answers to the most pressing research questions and potential mitigation measures.

RELATED PROJECTS

All of the projects reported in the papers generated for this effort are interrelated.

PUBLICATIONS

Cranford, Ted W., Megan McKenna, Melissa Soldevilla, Sean M. Wiggins, Jeremy Goldbogen, Robert Shadwick, Petr Krysl, Judy St. Leger, and John A. Hildebrand; **Anatomic Geometry of Sound Transmission and Reception in Cuvier's Beaked Whale (*Ziphius cavirostris*)**; **The Anatomical Record [in press, refereed].**

Mckenna, Megan F., Jeremy A. Goldbogen, Judy St. Leger, John A. Hildebrand, and Ted W. Cranford**; Evaluation of Postmortem Changes in Tissue Structure in the Bottlenose Dolphin (Tursiops truncatus); The Anatomical Record, 290:1023–1032 (2007). [published, refereed].**

Au, Whitlow W. L., Ronald A. Kastelein, Kelly J. Benoit-Bird, Ted W. Cranford, and Megan F. McKenna; **Acoustic Radiation from the Head of Echolocating Harbor Porpoises (*Phocoena phocoena*); The Journal of Experimental Biology, 209: 2726-2733 (2006). [published, refereed].**

Krysl, Petr, Ted W. Cranford, and John A. Hildebrand; **Lagrangian Finite Element Treatment of Transient Vibration/Acoustics of Biosolids Immersed in Fluids; International Journal for Numerical Methods in Engineering [in press, refereed].**

Cranford, Ted W., Wesley R. Elsberry, William G. Van Bonn, Jennifer A. Carr, Monica S. Chaplin, Diane J. Blackwood, Donald A. Carder, Tricia Kamolnick, Mark Todd, Sam H. Ridgway; **Observation and Analysis of Dolphin Sonar Signal Generation. Journal of Experimental Biology. [submitted].**

Wesley R. Elsberry, Ted W. Cranford, Diane J. Blackwood, Donald A. Carder, William G. Van Bonn, Jennifer A. Jeffress, and Sam H. Ridgway; **Measuring Intranarial Pressure during Biosonar; Journal of the Acoustical Society of America. [submitted].**

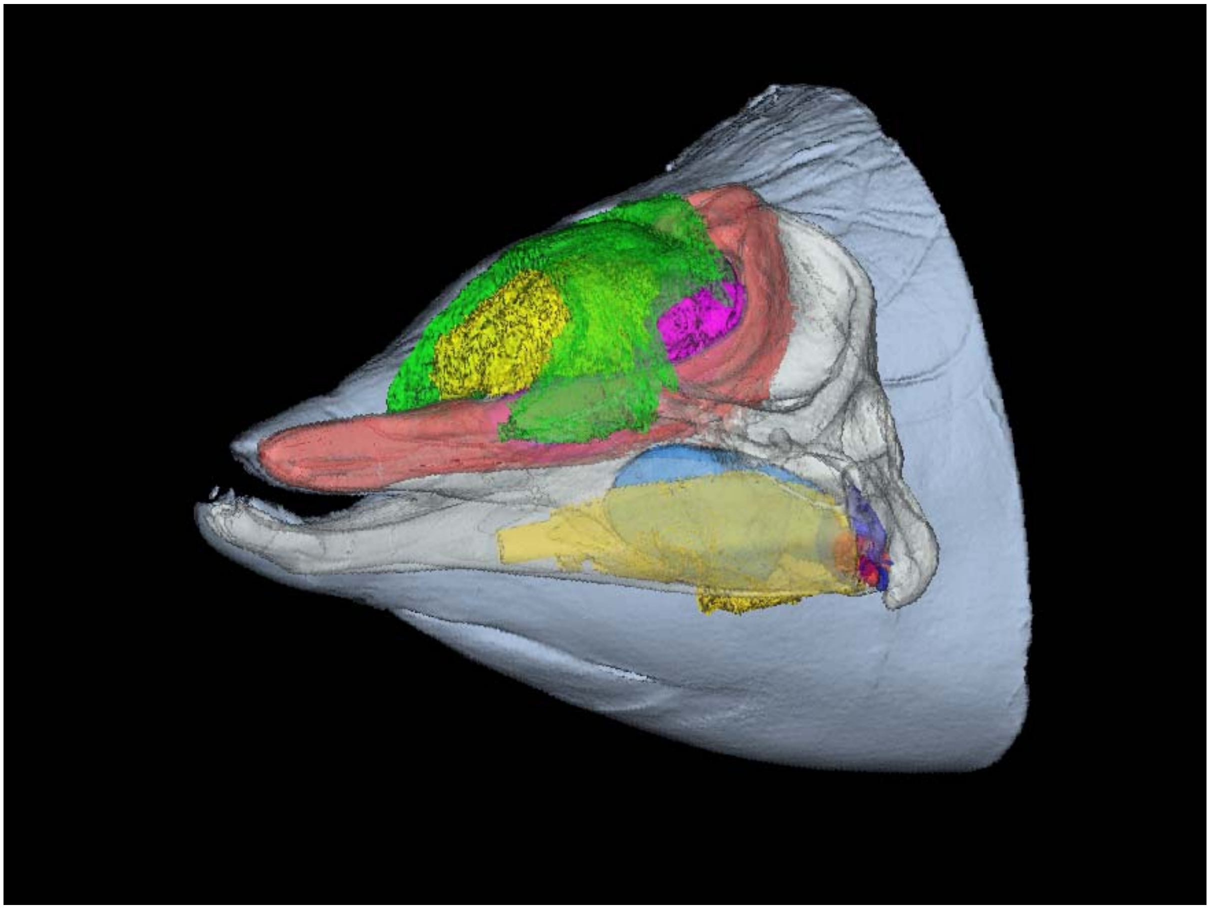
Ted W. Cranford, Petr Krysl, and John A. Hildebrand; **Acoustic pathways revealed: simulated sound transmission and reception in Cuvier's beaked whale (*Ziphius cavirostris*) using the vibro-acoustic toolkit; Bioinspiration & Biomimetics [submitted].**

Ted W. Cranford and Mats Amundin; **Dolphin Ear Trumpet Discovered: A New Acoustic Window into the Odontocete Ear; Nature. [submitted].**

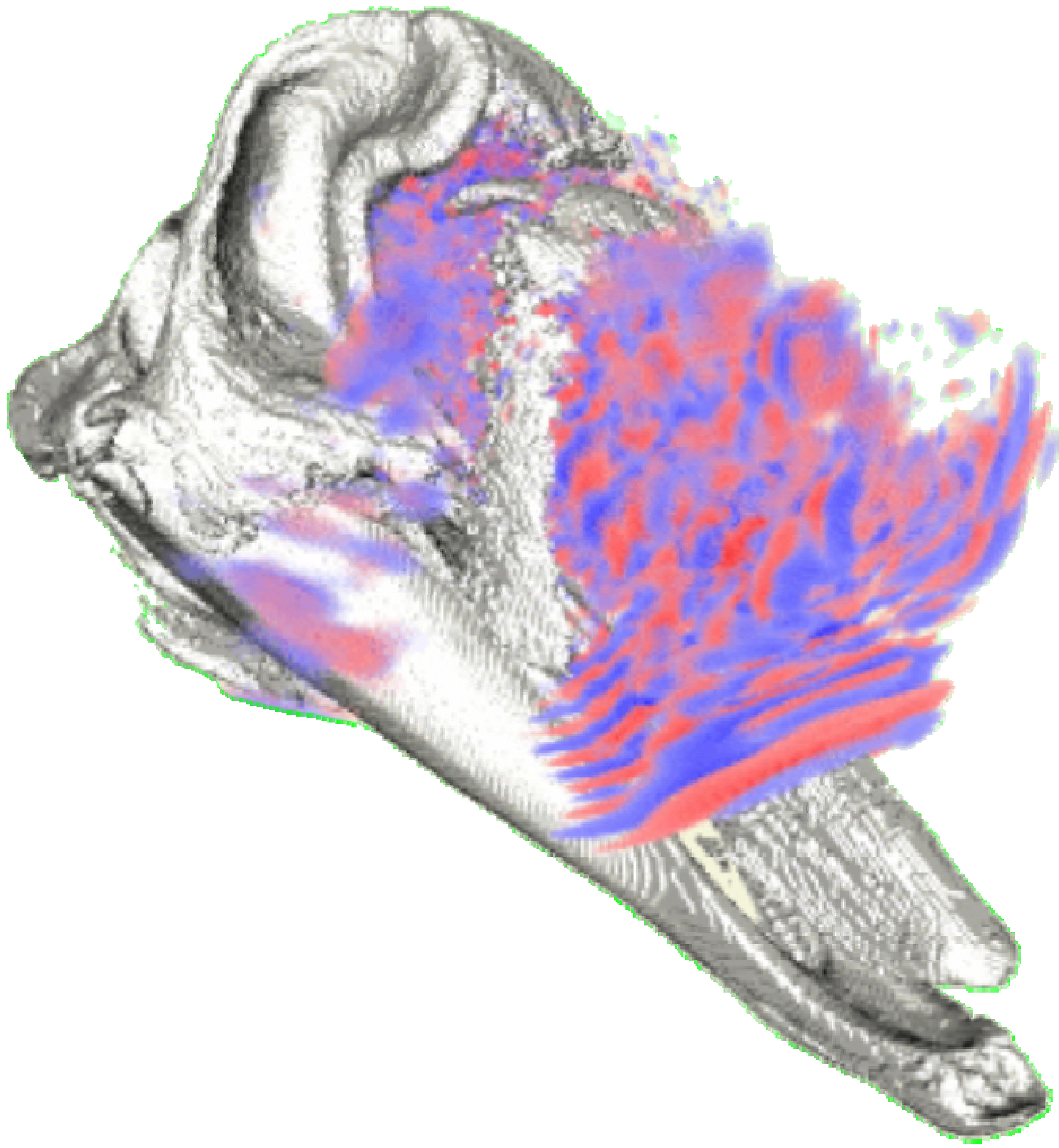
HONORS/AWARDS/PRIZES

Invited Oral Presentation. Conference: "The Effects of Noise on Aquatic Life" in Nyborg, Denmark (August 2007). Title: Sound Propagation in Cuvier's Beaked Whale (*Ziphius cavirostris*): A Test Case for Simulating Sound Propagation in Aquatic Organisms using FEM.

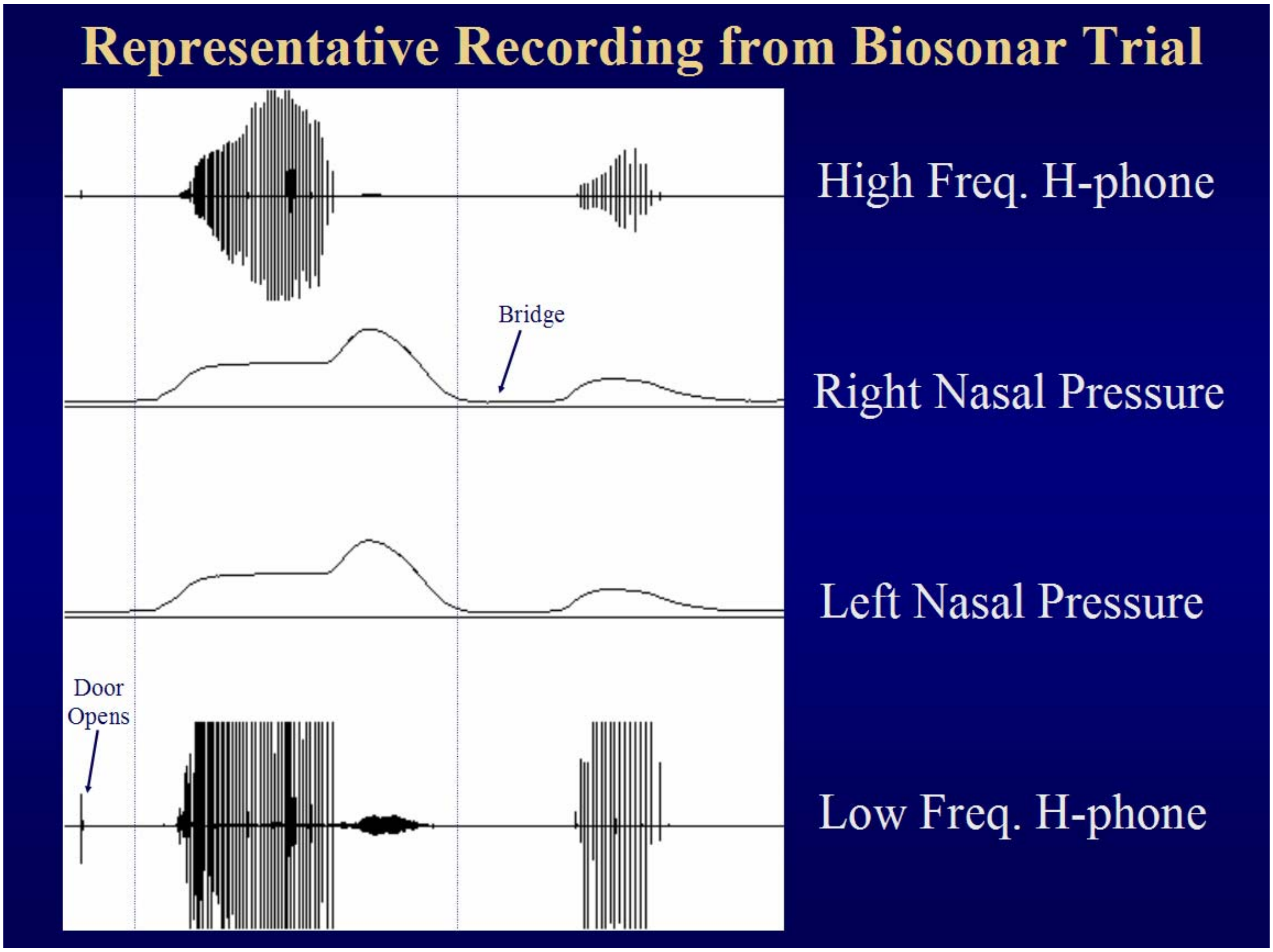
Sample Figures



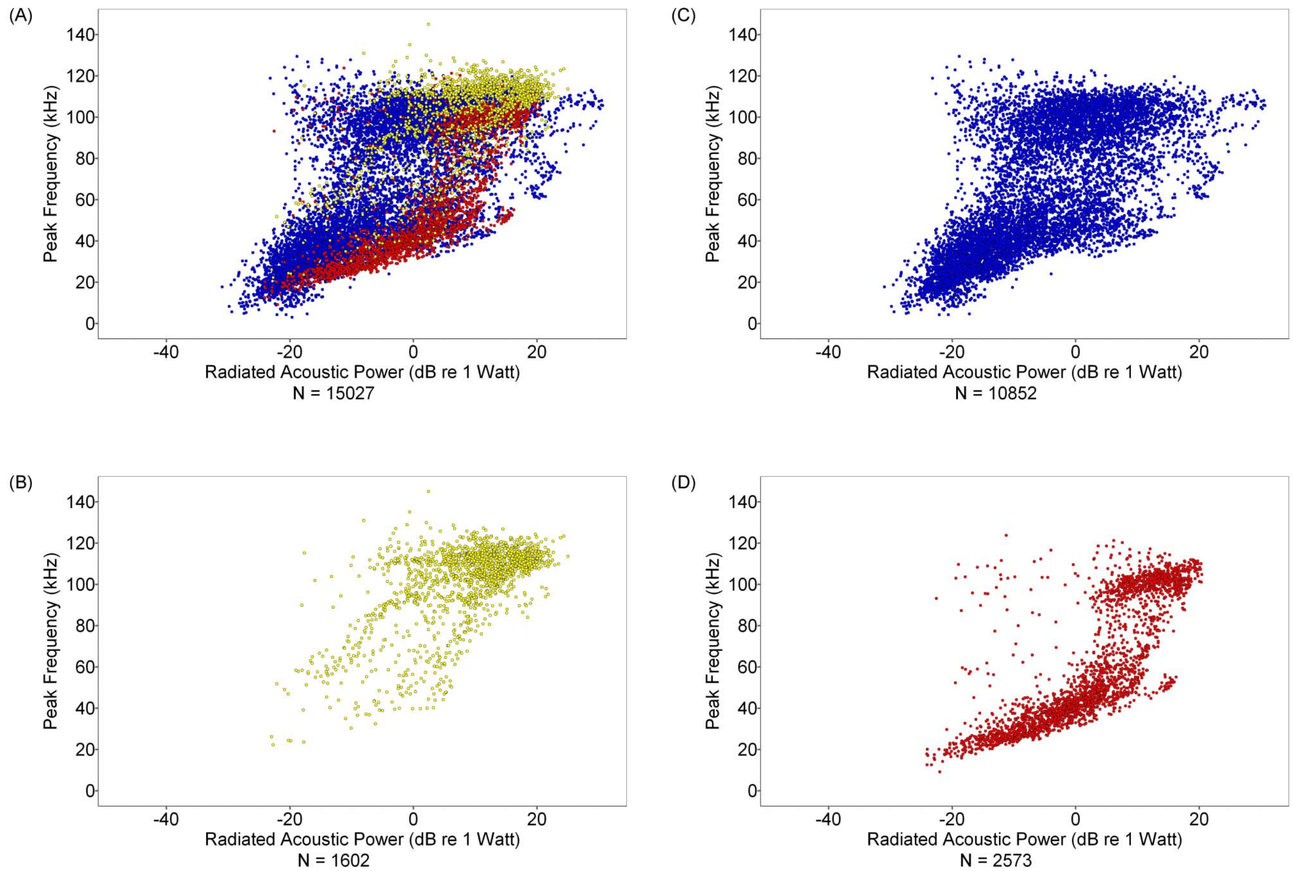
Three dimensional reconstruction from CT scans of the head of an adult male Cuvier's beaked whale (Ziphius cavirostris). Parts of the biosonar apparatus (top to bottom) have been colored to make them distinctive: Skin=light blue; Connective tissue theca=green; Melon=yellow; Low density fat body=magenta; Dense facial bones=orange; Bones=white; Mandibular fat body=gold; Air spaces=blue; Ear complex=red.



A sound beam produced from a source placed at the right phonic lips in a model of a Cuvier's beaked whale. Red indicates positive pressure, blue indicates negative pressure. Note that a planar wave front emerges from the head.



This figure shows a recording made during a biosonar target recognition task. Time is represented along the horizontal axis, approximately a 5 second sample. The top trace shows the acoustic pressure from a calibrated high-frequency hydrophone in the far field. The two middle traces show the pressure records within the right and left bony nasal passages, respectively. The bottom trace shows the record from a low frequency hydrophone. The events progress as follows: (1) The opening of an acoustically opaque screen, followed by (2) an increase in intranarial pressure over the basal nasal pressure, after a threshold pressure is reached, (3) The dolphin generates a click train and decides correctly that the target is present (4) She then increases the pressure dramatically to produce a whistle response, (5) The pressurization event ends as the pressure returns to the basal value. (6) Sometime later she receives the bridge and emits a short click train in celebration. The pressure always increases significantly prior to the onset of whistle production.



This figure shows peak frequency versus acoustic power from the biosonar clicks of three bottlenose dolphins during a target recognition task. The blue points are from the sonar clicks an adult female and are clustered into two distinct clouds at different frequencies. There is a weak trend toward higher frequency with increasing acoustic power. The red points show a similar pattern with low and high frequency clusters for an adult male. The yellow dots are from another adult female and indicate a different pattern, more likely to emit high-frequency clicks. She is also more economical than our other subjects, emitting fewer clicks per biosonar trial. If we pool the data for all three subjects, there are regions of overlap, but the individual differences are apparent.